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Luminance contrast in the background makes flashes harder to detect during saccades

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ABSTRACT

To explore a visual scene we make many fast eye movements (saccades) every second. During those saccades the image of the world shifts rapidly across our retina. These shifts are normally not detected, because perception is suppressed during saccades. In this paper we study the origin of this saccadic suppression by examining the influence of luminance borders in the background on the perception of flashes presented near the time of saccades in a normally illuminated room. We used different types of backgrounds: either with isoluminant red and green areas or with black and white areas. We found that the ability to perceive flashes that were presented during saccades was suppressed when there were luminance borders in the background, but not when there were isoluminant color borders in the background. Thus, masking by moving luminance borders plays an important role in saccadic suppression. The perceived positions of detected flashes were only influenced by the borders between the areas in the background when the flashes were presented *before* or *after* the saccades. Moreover, the influence did not depend on the kind of contrast forming the border. Thus, the masking effect of moving luminance borders does not appear to play an important role in the mislocalization of flashes that are presented near the time of saccades.

1. Introduction

While exploring a visual scene our eyes make many fast movements (saccades) to shift our point of gaze to objects of interest. During each saccade, the image of the world shifts across our retina. Under normal circumstances people do not perceive these shifts. The reduction in visual sensitivity during saccades that is responsible for the shifts themselves not being noticed is called saccadic suppression (e.g. Burr, Morrone, & Ross, 1994; Campbell & Wurtz, 1978; Ross et al., 2001; Shioiri & Cavanagh, 1989; Uchikawa & Sato, 1995; Watson & Krekelberg, 2009; Wurtz, 2008). Two kinds of mechanisms could contribute to saccadic suppression (reviewed in Castet (2010)): an active suppression driven by an extra-retinal corollary discharge and visual masking of the motion-blurred stimuli by the static images before and after the saccade. It seems likely that in normal high luminance contrast environments visual masking is the dominant mechanism (Castet, Jeanjean, & Masson, 2002; Wurtz, 2008).

Stimuli that were flashed on a uniform background during saccades were detected, even when their luminance contrast was just above threshold (Georg, Hamker, & Lappe, 2008). However, flashes presented during saccades on a background with a single additional rectangle of another color were not detected (Lappe et al., 2006). This difference implies that masking is very effective in suppressing vision during saccades, because a single rectangle of a different color is quite a minimal mask. Perhaps the fact that the border between the differently colored areas moves rapidly across the retina during the saccade makes the response to the flash harder to detect. However, we have recently shown that flashes presented during a saccade can be perceived despite large color differences in the background (Maij, Brenner, & Smeets, 2011). A difference between the studies that might be responsible for the difference in saccadic suppression is that we (Maij, Brenner, & Smeets, 2011) used isoluminant colored regions in the background, whereas Lappe and colleagues (2006) used a combination of color and luminance contrast. Do luminance borders specifically mask transient stimuli when they shift across the retina?

It is known for decades that visual objects presented briefly before, during or after saccades are systematically mislocalized (e.g. Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Maij, Brenner, & Smeets, 2009; Mateeff, 1978; Matin, Matin, & Pola, 1970; Matin & Pearce, 1965; Ross, Morrone, & Burr, 1997; Van Wetter & Van Opstal, 2008). Peri-saccadic mislocalization and saccadic suppression have been seen as related phenomena (Diamond, Ross, & Morrone, 2000; Michels & Lappe, 2004). The time courses of suppression and mislocalization support a common origin, which has been

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suggested to be the corollary discharge component of saccadic suppression (Diamond, Ross, & Morrone, 2000; Michels & Lappe, 2004). However, if suppression is mainly due to masking (Castet, 2010) and mislocalization is mainly due to the way in which retinal and extra-retinal signals are combined (Maij, Brenner, & Smeets, 2011; Morrone, Ross, & Burr, 1997), the two phenomena cannot be very tightly related.

Of course they will not be completely independent, for instance because backward masking is enhanced by corollary discharge signals (Ibbotson & Cloherty, 2009; Ibbotson & Krekelberg, 2011), but is there any evidence that luminance borders sweeping across the retina influence peri-saccadic mislocalization in a manner that can be linked to their effect on saccadic suppression?

In this experiment we directly compare the effects of isoluminant color borders in the background with the effects of luminance borders in the background on the perception of flashes presented around the time of saccades. The flashes always differ from the background in both color and luminance. We also investigated whether the flash's location relative to the border is critical: does it matter whether the border shifts across the flash location just before or just after the presentation of the flash?

2. Methods

2.1. Subjects

We conducted the experiment in a room illuminated by light from several fluorescent lamps. Six subjects volunteered to take part in the experiment (including one of the authors). Only the author was aware of the specific conditions. All subjects had normal or corrected-to-normal vision. The study is part of a research program that was approved by the ethics committee of the Faculty of Human Movement Sciences.

2.2. Experimental setup

Visual stimuli were presented on a touch screen (EloTouch CRT 19 in., 1024 × 768 pixels, 36 × 27 cm, 85 Hz) using the Psychophysics Toolbox in MATLAB (Brainard, 1997). The screen was orthogonal to the line of sight, at a distance of 50 cm and subtending 40° × 30° of visual angle. Eye movements were registered using an Eyelink II (SR Research Ltd., Mississauga, Ontario, Canada) at a sample frequency of 500 Hz using the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002). Subjects were asked to follow a 0.5° diameter jumping dot with their eyes. The dot was presented at a new position every 400 ms. It jumped in steps of 12° across the screen. All except the last jump displaced the dot randomly in one of eight radial directions: horizontal, vertical and diagonal (but never choosing a direction that would bring the dot within 115 pixels of the edge of the screen). The last jump of the dot was always a horizontal one, it either started 6° to the left of the midline and ended 6° to the right or vice versa.

After a series of 3, 4, 5 or 6 jumps (random with equal probabilities) a 0.5° × 12.3° vertical bar was flashed for one frame at one of three different locations. The locations of the flashed bar were defined with respect to the 12° displacement between the last two positions of the dot. The flash was presented along an invisible line through these positions, at −20%, 20%, or 130% of the dot's last jump. The dot was removed 50 ms after the last jump, which usually took place before the flash presentation. The trial ended when the subject indicated where he or she had perceived the flash by touching the screen at that location. The subject was instructed to touch a corner of the screen if he or she did not perceive the flash.

The backgrounds could consist either of three segments (red and green or black and white), or could be uniform. If the background consisted of three segments, there were two segments of one color at the two sides, with a segment of a different color or luminance extending vertically across the whole screen between them. The central segment extended horizontally from the dot's position before the last jump (6° from the midline) to a position beyond the saccade target (8.4° to the opposite side of the midline; see Fig. 1). We presented a red jumping dot and a green flashed bar (of the same luminance) on black and white backgrounds, and we presented a black jumping dot and a white flashed bar on (isoluminant) red and green backgrounds.

On trials with a border, for the −20% location of the flash, a border passed the flash's retinal location almost immediately after the flash if the flash was presented during the saccade. For the other two flash locations the border passed the flash's retinal location just before the flash. For the 20% flash location the expected *percept* did not cross the border, whereas for the other two it did.

There were eight possible backgrounds (Fig. 1), but we will not consider distinctions between red (44 cd/m^2; CIE_{xy} = 0.59, 0.35) and green (matched individually to red in luminance; CIE_{xy} = 0.29, 0.57) or between black (8 cd/m^2) and white (126 cd/m^2; CIE_{xy} = 0.28, 0.32) except in forming the borders, so we only consider there to be two patterns for the red–green and for the black–white surfaces: uniform or segmented. These four combinations (uniform red–green; segmented red–green; uniform black–white; segmented black–white) will be referred to as conditions. Isoluminance for red and green was determined individually by flicker photometry.

2.3. Calibration

Before each session the subject was asked to calibrate the Eyelink II using the standard nine-point calibration procedure. To synchronize the eye movement recordings with the images presented on the screen, we presented two flashes at the same time. One of them was the flash that the subject had to localize. The other flash (in the lower right corner of the screen) was used to synchronize the eye movement recordings with the images presented on the screen, and was not visible to the subject. We measured the moment of this second flash with a photo-diode that was attached to the lower right corner of the screen. The photo-diode sent a signal to the parallel port of the Eyelink computer. This signal was registered in the data file on the Eyelink computer. The temporal relationship between such a record and the record of the eye orientation at the moment of the flash was previously determined by using the photo-diode to drive an infrared lamp that 'blinded' one of the Eyelink's infrared cameras. Because the photo-diode was placed in the lower right corner, and the flash was presented at different locations on the screen, the real timing was only known to within a few milliseconds (we did not correct for the temporal effects of variation in the position of the flash on the screen). For trials in which no signal was registered on the parallel port (due to technical failure; 3% of all trials) we used the average delay (14.9 ms) between the record of the command to show the flash (that was also recorded on the Eyelink computer) and the record of the signal on the parallel port on trials in which there was such a signal, to estimate when the flash had occurred.

2.4. Procedure

Because the suppression of the flash only occurs around the moment of the saccade, we wanted to present as many flashes as possible at about that time. We used the saccadic reaction times on previous trials to predict the saccade onset (Maij, Brenner, & Smeets, 2009). At the predicted saccadic reaction time the bar was flashed on the screen for one frame at one of the possible flash locations (defined in relation to the last displacement of the dot).

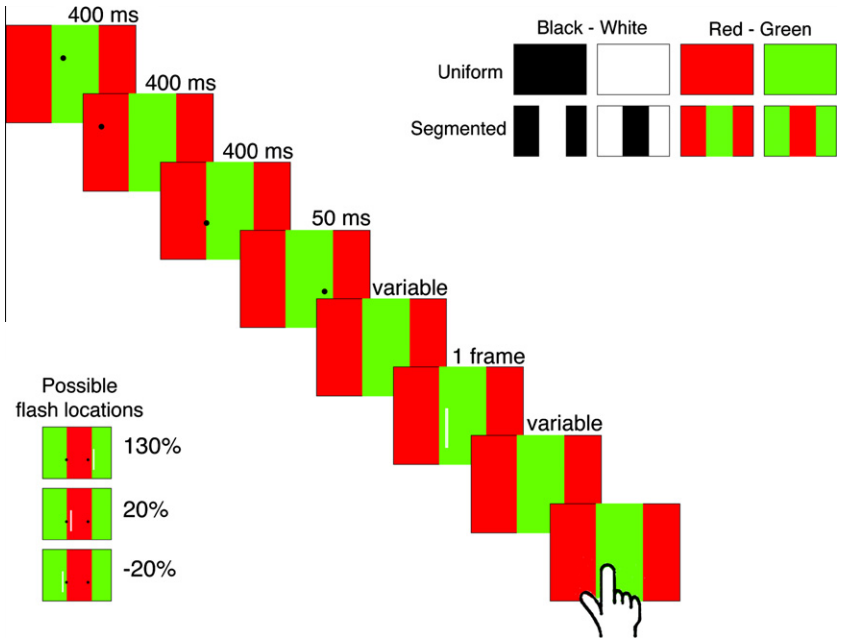

Fig. 1. Schematic overview of an example trial with a rightward saccade, red–green segmented background, and a flash at 20%. The displacement between the last two positions of the dots was always 12° (representing 0% and 100%). The flash was presented at the anticipated moment of the saccade (based on the saccadic latency on previous trials). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The subjects were asked to touch the screen at the location at which they saw the flashed bar. If no new dots appeared and the subject had not seen a bar (for instance because the flash was suppressed), the subject indicated having missed the flash by touching a corner of the screen.

2.5. Sessions

Subjects performed four sessions of 600 trials each. In each session all conditions were presented equally often, in random order.

2.6. Data analysis

We used the *Eyelink's gaze position data* of the right eye to determine various characteristics of the saccades. For an eye movement to be considered to be a saccade, its tangential velocity had to exceed 35°/s for at least two consecutive samples (4 ms). The saccade end was defined as the first sample for which the tangential velocity was below 35°/s. We discarded trials if the length of the saccade was less than 60% or more than 140% of the displacement of the dot. Trials were also discarded if the direction of the saccade was not between ±22.5° of horizontal. Furthermore, we discarded trials in which the subject did not make a saccade near the time of the flash (i.e. if there was no saccade onset from 80 ms before the flash until 60 ms after the flash).

We only used the first location at which the finger touched the screen. We discarded trials in which the touched location differed from the flash location by more than 10° (of visual angle) in the direction of the saccade, 6° in the opposite direction than the saccade or 6° orthogonal to the direction of the saccade. We also discarded trials in which the subject touched the corner of the screen to indicate that he or she did not perceive the flash. For all other trials, the touched location was regarded as the perceived location.

2.7. Saccadic suppression

For each subject and condition we made bins of 10 ms in the time of the flash with respect to saccade onset, and determined the fraction of missed flashes for each bin. We ignored bins for which there were fewer than three trials. We then averaged the bins across subjects, and removed bins at times for which we had data for fewer than five subjects.

2.8. Mislocalization

We only consider horizontal mislocalization. We plotted the horizontal component of the vector between the touched location and the true location of the flash, as a function of the time of the flash relative to saccade onset. To draw a smooth curve through the data (for a representative subject) we averaged the errors for each condition and flash position with weights based on a (moving) Gaussian window (σ = 10 ms). The smooth curve was drawn as long as there were at least five data points within $\pm\sigma$ of the peak of the Gaussian. We will refer to this curve as the mislocalization curve.

In order to compare mislocalization with saccadic suppression, we defined a measure for the *fraction of mislocalized flashes*. We defined the *fraction of mislocalized flashes* as flashes that were misperceived in the horizontal direction (towards the saccade target) by more than 20% of the saccade amplitude. For a flash at −20% on a segmented background, a mislocalization of more than 20% of the saccade amplitude in the direction of the saccade corresponds with a shift in the perceived position of the flash onto a part of the background that has a different color. For each subject and condition, we made bins of 10 ms in the time of the flash with respect to the saccade onset. For each bin we determined the fraction of the detected flashes that were mislocalized according to the above-mentioned definition. The same criteria were used for including bins as we used for saccadic suppression. For each subject and condition, we also determined the mean signed localization error (bias) for all detected flashes 35–60 ms before and 50–70 ms after the saccade.

3. Results

We obtained useful *saccades* on 54 ± 10% of the trials in the segmented red–green condition, 52 ± 9% of the trials in the uniform

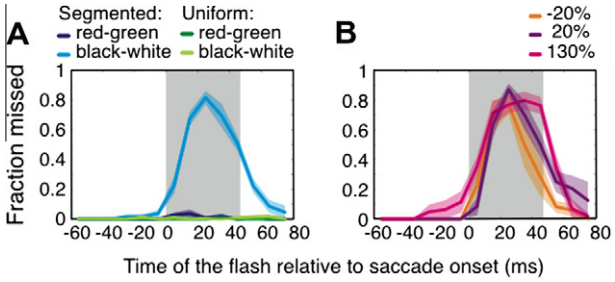

Fig. 2. Average fraction of missed trials. Transparent bands: standard error of the mean (across subjects). Gray bar: average saccade duration. (A) Fraction of missed trials for the four different conditions irrespective of the flash location. (B) Fraction of missed trials in the black–white segmented condition for the three different flash locations.

red–green condition, 56 ± 10% of the trials in the segmented black–white condition and 54 ± 9% of the trials in the uniform black–white condition (means ± standard errors across participants).

3.1. Saccadic suppression

Subjects missed the flash on up to 80% of the trials when the flash was presented during the saccade on the black and white segmented background (Fig. 2A). In the other conditions (red and green segmented condition and both uniform conditions) the fraction of trials in which the flash was missed was negligible. The fraction of missed trials did not differ between the three different flash locations for the black–white segmented background (see Fig. 2B), despite the difference in when the segment border passed the flash location on the retina (just after the time of the flash for the −20% flash location and just before the time of the flash for the other two flash locations, if the flash was presented during the saccade).

3.2. Mislocalization

Subjects readily perceive flashes on a different background color (Maij, Brenner, & Smeets, 2011; see Fig. 3A). For flashes that were detected, the fraction of localization errors that was larger than 20% of the saccade amplitude was similar for the red–green backgrounds and the black–white backgrounds (compare light and dark versions of the same color in Fig. 3B and C). There were, however, some systematic differences between uniform and segmented backgrounds, especially for flashes presented before and after the saccades (compare the two colors in Fig. 3B and C). The fraction of mislocalized flashes showed a different dependence on the time of the flash for each flash location (see Fig. 3D).

There was a significant influence of the presence of the border (uniform versus segmented; averaged across black–white and red–green backgrounds) on the localization bias for flashes at 130% presented both before ($t_{10} = 2.31$; $p < 0.001$) and after ($t_{10} = 8.53$; $p < 0.05$) the saccade. It is surprising that the perceived position of the flash is influenced by the border at this flash location when the flash occurred after the saccade. In that case the eyes were already oriented towards a position near the flash location when the flash occurred, so the effect of the border cannot be a simple consequence of improving trans-saccadic integration (Deubel, Schneider, & Bridgeman, 2002; Niemeier, Crawford, & Tweed, 2003).

A possible reason for finding systematic errors for flashes presented at the 130% location (the location nearest to the saccade target) is that subjects localize the flashed target relative to the nearest stable landmark (which was the saccade target for that flash location) and assume that their eyes landed on the – by then invisible

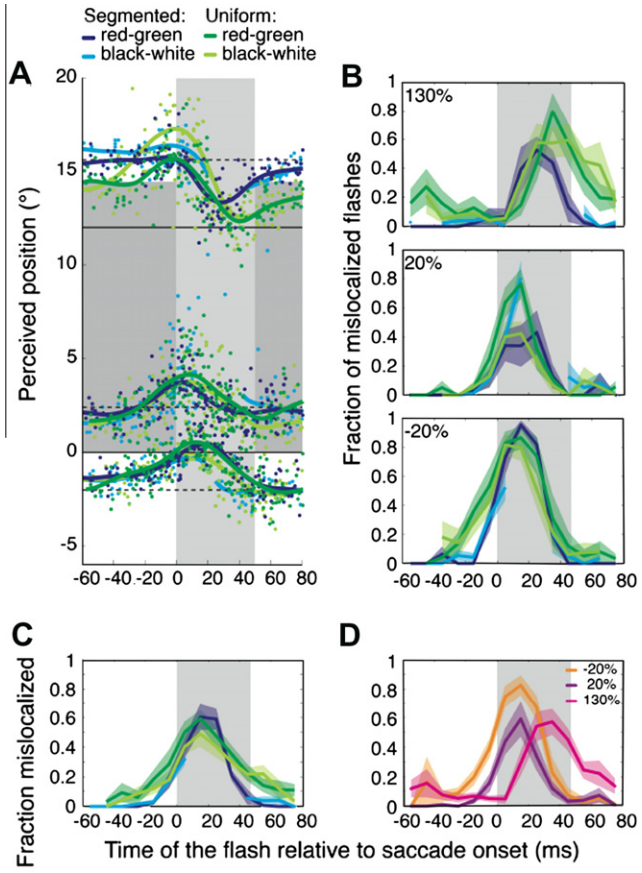

Fig. 3. (A) Mislocalization curves of one subject. The dots show errors for individual flashes. The curves are smoothed averages of the dots of the same color. Dark gray area: region that could have a different color or luminance. Dashed lines: the three flash positions. Light gray bar: average saccade duration. Horizontal solid line at 0°: saccade start location. Dashed horizontal line: saccade target location. (B) Average fraction of mislocalized flashes: flashes for which the horizontal location was misjudged by more than 20% of the saccade amplitude towards the saccade target. Transparent bands: standard error of the mean (across subjects). Gray bar: average saccade duration. Panels: different flash locations. Some of the curves are not continuous, because not enough flashes were perceived at certain times. (C) Average fraction of mislocalized flashes for the four conditions, irrespective of the flash location. Transparent bands: standard error of the mean (across subjects). (D) Average fraction of mislocalized flashes for the three flash locations, irrespective of the condition. Transparent bands: standard error of the mean (across subjects). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

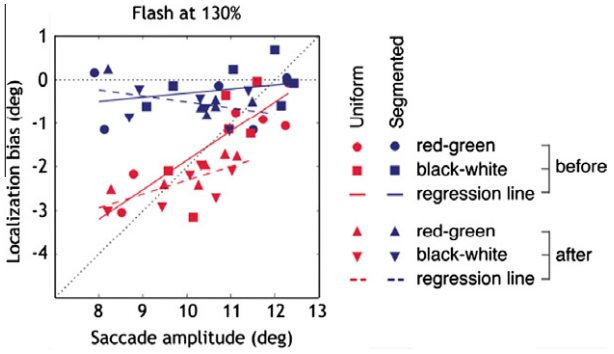

Fig. 4. Correlation between the localization bias and the saccade amplitude for the 130% flash location. Each symbol represents the mean bias and saccade amplitude of one subject in one condition. Circles and squares indicate the means of trials in which the flashes were presented 35–60 ms before saccade onset. Triangles indicate the means of the trials in which the flashes were presented 50–70 ms after saccade onset. The diagonal dotted line indicates a localization bias that is proportional to the error in the saccade amplitude.

– saccade target even if they did not (and interpreted the retinal information accordingly). One would only expect subjects to systematically misjudge the amplitude of the eye movement in this manner if there are no clear landmarks near the saccade endpoint, so if this reasoning is correct we only expect to find such localization biases in the uniform conditions. The data of the example subject in Fig. 3A suggests that this may be the case, so we examined whether the systematic errors are correlated with the saccade amplitudes for the uniform conditions; and whether they are not for the segmented conditions. This is indeed what we found (Fig. 4). We found a significant correlation between saccade amplitude and bias both for flashes presented before ($p < 0.001$, $r = 0.83$) and after ($p < 0.01$, $r = 0.73$) the saccade for the uniform backgrounds.

4. Discussion and conclusion

We studied the influence of luminance and color contrast in the background on the perception of flashes that are presented near the time of a saccade. We found that if the background had black and white segments, subjects missed many flashes that were presented during the saccade (Fig. 2). This is in line with our interpretation of the various previous findings discussed in the introduction (Lappe et al., 2006; Maij, Brenner, & Smeets, 2011) in terms of the luminance contrast that sweeps across the retina during saccades masking flashed stimuli. We did not find an effect of the location of the presented flashes on saccadic suppression. Thus, it does not appear to matter whether the border passed the flash's retinal or perceived location just before or after the flash; the flash is not only masked when it is immediately followed by a transient signal at the same location.

It is known for decades that the locations of objects presented briefly near the time of saccades are systematically misjudged (e.g. Bischof & Kramer, 1968; Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Maij, Brenner, & Smeets, 2009, 2011; Matin & Pearce, 1965; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). We found no clear effect of the presence of borders on the mislocalization of flashes presented during the saccade (Fig. 3C). We only found effects of the border on localization when the flashes occurred before and after the saccade. In particular, we found smaller systematic localization errors for flashes near the saccade target when a border was present. The latter finding is consistent with the finding that flashes that are presented beyond the saccade target are localized more accurately when the saccade target is present during the whole trial than when the saccade target is only briefly visible (Maij et al., 2010).

Our study does not support the idea that suppression and mislocalization are related processes (Diamond, Ross, & Morrone, 2000; Michels & Lappe, 2004). During saccades, flashes were suppressed when there was a black–white segmented background but not when there was a red–green segmented background (Fig. 2). Nevertheless, the mislocalization of perceived flashes was similar for the two conditions with segmented backgrounds (including presentations around saccadic onset, Fig. 3C). The luminance contrast in the background therefore appears to influence suppression without affecting localization. Furthermore, the time–course of mislocalization (Fig. 3) and the time–course of saccadic suppression (Fig. 2) are different in our study. The fraction of missed trials is elevated from saccade onset until 80 ms after the saccade, whereas the fraction of trials that were mislocalized horizontally by more than 20% of the saccade amplitude is elevated from 20 ms before saccade onset until the end of the saccade (at least for the flashes at −20%). Moreover, the time at which the subjects started mislocalizing the flashes depended on the flash location (Fig. 3D) whereas the fraction of missed flashes did not show a clear dependence on flash location (Fig. 2B).

That subjects use visual references to localize briefly presented objects has been shown in many studies (e.g. Dassonville, Schlag, & Schlag-Rey, 1995; Honda, 1993; Maij et al., 2010). The role of the saccade target has been investigated before and it has been shown that subjects use the relative distance between the saccade target and the flash location to localize the flash (Maij et al., 2010). In our study the saccade target is only shown briefly (50 ms), so its role as a reference point is very limited. We found a correlation between the saccade amplitude and the localization bias for the uniform backgrounds (Fig. 4), suggesting that subjects assume that their eyes landed on the saccade target when the flash was presented beyond the saccade target, even when the eyes did not. In this context, it is not surprising that other landmarks, such as the border, can help localization.

To summarize, we confirmed that the motion of luminance contrast across the retina during saccades makes briefly presented stimuli harder to detect. Purely chromatic contrast did not have such an effect. This is somewhat surprising, because it has been suggested that the magno-cellular pathway is actively suppressed during saccades (Burr, Morrone, & Ross, 1994; Han, Xian, & Moore, 2009; Uchikawa & Sato, 1995), so one may have expected the effects of luminance contrast in the background to have been suppressed during the saccade. Apparently there is enough stimulation of the magno-cellular pathway by the moving border to make it impossible to detect the flashes during the saccades, despite the flashes always having a different color than the background as well as a different luminance. Indeed, there is both behavioral (Castet, Jeanjean, & Masson, 2002) and neurophysiological (Ramcharan, Gnadt, & Sherman, 2001; Reppas, Usrey, & Reid, 2002) evidence that the reduced sensitivity to stimuli presented during saccades is not simply caused by an overall inhibition of activity at an early stage of the magno-cellular pathway. In addition to the effects on detection, we show that the borders between the segments are used as visual references before and after the saccade (at least for a flash at 130% of the saccade amplitude). We argue that the detection and the localization of flashes are not as tightly connected as one may expect.

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